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Heterothallism and hypothetical hormones in Neurospora

B. O. Dodge

(with a text figure)

There is a controversy of many years standing among mycologists as to whether in such forms as *Pyronema* and the Erysiphaceae an act of fertilization precedes the formation of ascocarps. Professor and Madame Moreau[1] have recently questioned the possibility of such a process at the origin of perithecia in species of *Neurospora*. In a more recent preliminary note, Moreau and Moruzi[2] have described an interesting culture experiment in which the U-tube plays an important rôle. It is claimed that their results further support the doctrine of the absence of a copulation at the origin of the ascocarp. The U-tube is a familiar piece of apparatus to students of physics and chemistry, and it is often used in experiments with bacteria and yeasts where the evolution of gases is being studied. Its use in an attempt to settle the puzzling questions of sexuality and heterothallism in the fungi is something new.

The Moreau-Moruzi U-tube experiment

The culture tube was provided with two arms *M* and *N* of large diameter, while the median connecting portion was of smaller diameter (fig. 1). The culture medium was corn meal agar, upon which species of *Neurospora* fruit abundantly when mated. The experiment was carried out with two races of *Neurospora*. The race sowed in arm *M* was an orange-colored *Monilia* mold found in mushroom beds. It appeared to be the *Monilia* stage of a species of *Neurospora*. The race sowed in arm *N* was a strain of *N. sitophila* obtained from the writer. They had previously proved that these two races, sowed separately, produced only little sclerotia, but sowed together in the same Petri dish culture they produced perithecia with asci and ascospores. After some days ('au bout de quelques jours') small sclerotia were formed in each branch *M* and *N*, and then fertile perithecia developed, but only in the arm *M*. At first it was thought that the mycelium from the arm *N* had grown down around to mix with that in arm *M*. This was proved not to be the case in the following way.

As soon as perithecia appeared in *M* a section 'a–b' of the median portion of the tube was cut out and placed in a sterile damp chamber. The arm ends *M* and *N* were also placed in sterile containers. No growth ever

[1] Moreau, Fernand, et Mme. Moreau. Le développement du périthèce chez quelques Ascomycètes. Rev. Gén. Bot. **42**: 65–98. 1930.

[2] Moreau, Fernand, et Mlle. C. Moruzi. Recherches expérimentales sur la formation des périthèces chez les "*Neurospora*." Compt. Rend. Acad. Sci. Paris **192**: 1476–1478. 8 June 1931.

[The Bulletin for November (**58**: 465–516) was issued 24 December 1931.]

appeared in the section 'a–b'. After some days hyphae with conidia developed at the freshly cut ends of the *M* and *N* pieces. Conidia from these two sources were sowed separately, but the cultures developed no perithecia. Sowed together in the same Petri dish, perithecia with asci matured. This would seem to prove that the race cultured at *M* was not hermaphroditic. The characters of the asci and spores produced would have determined this point more certainly, but these details are not given.

Since it was proved that no hyphae passed from *N* to *M*, these authors conclude that there can be no act of copulation at the origin of the perithecium. There must be something developed analogous to hormones ('harmozones') which, diffusing through the agar in advance of the mycelial growth, induces the incipient perithecia in *M*, represented by sclerotia, to continue on to mature perithecia. Heterothallism in *Neurospora*, then, they conclude, is nothing more than a matter of diffusible hormones. The real act of fecundation occurs when two nuclei fuse in the ascus.

SOME GENERAL CONSIDERATIONS

We are all modifying our old notions as to the nature of sex in animals and higher plants. While using the terms sex and sexuality for convenience in describing the phenomena attending reproduction in *Neurospora* and *Ascobolus*, the writer has tried to avoid expressing himself very definitely on this question, being more content to learn what really happens, or what kinds of progeny are produced, when two different races or species are grown together in a culture. He has frequently pointed out that perithecium-like bodies are often produced in single spore cultures of the heterothallic species of *Neurospora*. From what we know of other ascomycetes it would not be surprising to find that these structures could be stimulated to produce asci under some particular conditions. When in the past, however, such bodies have been crushed the central region has always been found to be composed of a mass of empty cells. If asci develop in single spore cultures it must be a rare occurrence.

When the unisexual components, S_1 and S_6, of the hermaphroditic species *Neurospora tetrasperma* are grown from opposite sides of a Petri dish culture, perithecia are usually formed only on the S_6 side. Although it has not been possible to demonstrate clearly that hyphae from the side S_1 pass over onto the S_6 area it has always been obvious[3] that in some way the elements of inheritance from S_1 must be brought to each point where perithecia are formed on S_6. Not having any cytological proof, one might well hesitate before suggesting that, starting with anastomoses between hyphae

[3] DODGE, B. O. Material for demonstrating sexuality in the ascomycetes. Torreya **30**: 35–39. 1930.

of S_1 and S_6, there might be a wandering of nuclei from the S_1 hyphae back through the S_6 hyphae to account for the peculiar distribution of fruit bodies in such cultures[4].

Culturing the eight progeny from a single ascus will convince anyone that whatever it is that enables one mycelium so to influence another that perithecia will mature asci, it must be something that is associated with chromosomes in order to be segregated out at reduction in such a perfect Mendelian ratio. To carry out the idea of Moreau and Moruzi a little farther, may it not be that the genes for the Mendelian inheritance of morphological characters are also diffusible hormones? If one would grow a typical orange-colored conidial race of *Neurospora sitophila* in one arm which we may call arm $+C$ of our U-tube (fig. 1), and an albino non-conidial race of the opposite sex in the other arm $-C$, what kind of perithecia, if any, may one expect to obtain in the $+C$ arm, and what kind, if any, in the $-C$ arm?

RESULTS OF OUR OWN U-TUBE EXPERIMENTS

With the above question in mind, a number of U-tube experiments were carried out. For this purpose some of the tubes were patterned after the one described by Moreau and Moruzi. Others were more nearly V-shaped, and still others were of all sorts of shapes and sizes. The culture medium employed was corn meal agar varying in hardness up to 2 per cent. In some cases a corn meal decoction was first poured in to fill the median cross arm of the U-tube, and then corn meal agar was carefully poured in to harden on top of this. A corn meal gelatin medium was also tried out, but the gelatin is quickly liquified by *Neurospora*, and it is not a favorable medium for the production of perithecia even in mixed cultures.

The races of *N. sitophila* cultured were all derived from ascus no. 56, which was discussed in the paper previously cited[4]. By growing an orange-colored conidial race, either 56.7 or 56.8, in one arm, and an albino non-conidial race, either 56.1 or 56.2, in the other arm one had in his U–tube two mycelia which could be easily distinguished and which were of opposite sex. The reciprocal relationship was obtained when the albino non-conidial race, either 56.5 or 56.6, was grown in one arm and the orange-colored conidial race, either 56.3 or 56.4, in the other arm. Fifty such U–tube cultures, inoculated with the one or the other of these combinations, were prepared and kept under observation, in many cases for two or three months. Twelve U–tube cultures inoculated with the races S_1 and S_6

[4] See plate 7, figs. 15, 17 in DODGE, B. O. The inheritance of the albinistic non-conidial characters in interspecific hybrids in *Neurospora*. Mycologia **22**: 265–334. 1931.

of *N. tetrasperma* were also grown for a long time.[5]

The experiment was varied by growing strains 56.8 and 56.1 separately in flasks containing corn meal broth for five or six days. During this time the same strains were grown separately on corn meal agar in ordinary culture tubes. The broth now presumed to contain the hormones was put through a Berkefeld filter, grade *N*, and some of the filtrate was introduced into the tube cultures. The customary checks were maintained. The particular filtrate introduced in each case was chosen with due regard to the sex of the mycelium in the culture tube, the filtrate from flask 56.8 going into tubes 56.1, and filtrate 56.1 into tubes 56.8. Thirty such cultures were prepared. Another set was made using strains S_1 and S_6.[5]

Mycelia that had been grown on broth were killed by steaming and then placed in plate cultures in which a mycelium of the opposite sex in each case had been growing for one week. This was done on the theory that dead fungous cells would give off the hormones as has been claimed for the higher plants.

The results of these experiments, so far as confirming the hormone theory of heterothallism in *Neurospora* proposed by Moreau and Moruzi is concerned, were entirely negative. As long as the two living mycelia do not meet in the presence of air, no perithecia are formed. Soon after the inoculations are made, hyphae begin to grow downward at a rate that seems to depend on how much absorbed air remains in the agar after sterilization. If the U–tube is dry-sterilized previously and the agar medium that has been held in tubes for some days is melted and poured into the U–tube, less oxygen is driven off. The hyphae from the opposite arms then usually grow downward rapidly, slowing up when about to meet somewhere along the median connecting arm (fig. 1, left). It is unnecessary to cut out a piece of the median portion of the tube to prove that the mycelia do not pass each other. With properly prepared agar one can see what goes on with a hand lens. Very few anastomoses occur between hyphae from the two sides in the absence of free air even though their end branches may intermingle somewhat. When two strains of opposite sex are grown in Petri dish cultures, one sees many anastomoses where the hyphal branches meet. In case most of the air has been boiled out of the agar through autoclaving or intermittent sterilization after the U–tubes have been filled, the hyphae do not grow downward very far, so there is apt to remain several centimeters of agar in the connecting arm entirely free from hyphae, even though the culture has been kept two or three months. If the medium in only one arm of the U–tube is inoculated, the mycelium grows down and around rapidly, and soon appears at the surface of the medium in the

[5] Later on these experiments were repeated varying the conditions somewhat, but with the same results in every case.

other arm, where conidia will be formed if it is conidial strain. When the medium in both arms has been inoculated, the mycelium present in one arm seems to prevent absolutely any hyphae in the other arm from growing around up in this fashion. No conidia, for example, have ever developed in the arm originally containing the $-C$ mycelium. Any ascocarps, then, that would be formed on the surface of the medium in either arm would have to be due either to the stimulus of something analogous to diffusible hormones, or to the wandering of nuclei brought into the unisexual mycelium as the result of anastomoses where the two mycelia of opposite sex

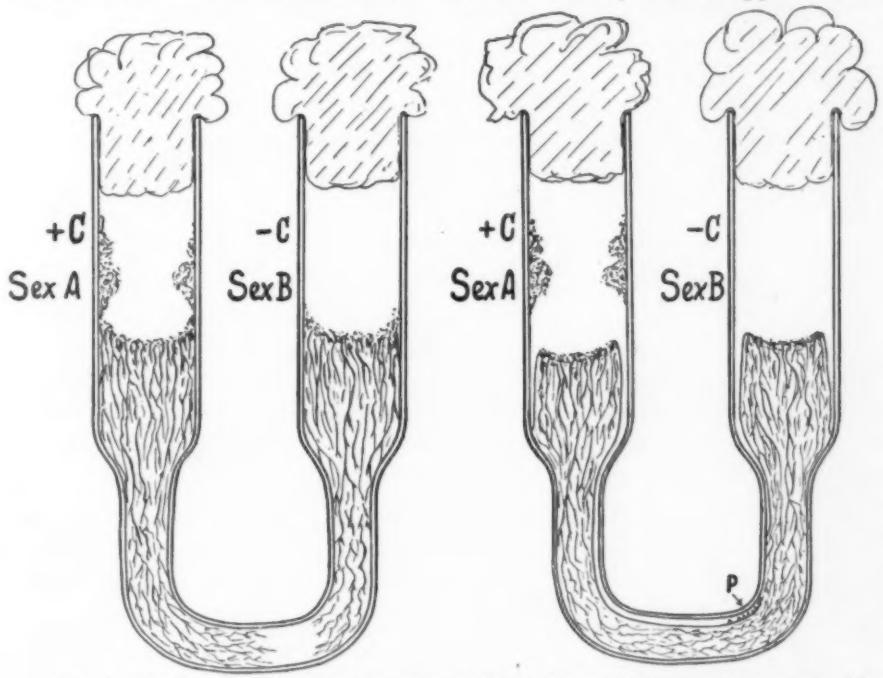

Fig. 1. Diagram of a section of one type of U-tube used. The position reached by the mycelia at the end of the first week is shown in the figure at the left. No further advance was apparent during the next eleven weeks. The figure at the right shows the air pockets due to drying of the agar during this time. Perithecia formed at *P* a few days after the air film reached this point.

may perhaps meet in the median connecting arm. No such perithecia have ever matured at the surface of the medium in either arm of our U-tubes. The explanation is clear from what follows.

After two or three weeks the agar in the side arms exposed to air usually begins to dry out and pull away from the glass (fig. 1, right). The hyphae that had ceased to grow downward then renew growth, keeping a little in advance of the layer of air that slowly makes its way down the side arms. This drying out usually occurs first in the arm containing the

conidial strain, perhaps because the production of masses of dry powdery conidia favors transpiration. In a U–tube of the pattern described by Moreau and Moruzi with a median arm of smaller diameter this drying out and pulling away of the agar does not extend into the connecting arm until after several weeks. The length of time depends upon the depth of the agar in the large side arms. It should be noted however that no perithecia are formed in any case until the drying out brings into the air pocket the mycelia of both sexes. Within a few days after this occurs perithecia always do form, but not at the top of the agar slant in the side arms. They first appear in the region down below where there is now an intermingling of the two mycelia in the presence of air (fig. 1, right). Perithecia may later form beneath the agar surface.

Five V–tubes were cut at the angle at the time when the two mycelia were about one centimeter apart at that point. The separated arms were kept in a sterile humid condition for two months without the formation of any perithecia. On the theory that hormones, by the laws of diffusion, would be distributed all through the agar, perithecia should have formed at the freshly broken surfaces a few days after exposure to air. In each case however, hyphae grew out and formed little sclerotia, but no perithecia ever matured, either at the freshly cut ends or at the surface of the original agar slants above in the large arms.

Whatever may be the rate at which the hypothetical hormones diffuse through agar media such as used here, as compared with the normal rate of growth of the mycelium under favorable conditions, by varying the amount of absorbed air and the amount of the agar medium in the U–tube one can so regulate the rate of growth as to enable any hormones given off by the mycelium at the surface of the medium in one arm of the tube to move downward faster than the hyphae. In some of our U–tubes hyphae from the two mycelia grew down so rapidly as to come within a few millimeters of each other within four or five days. In others the mycelia remained far apart for many weeks, or until the agar, by drying, pulled away from the glass and allowed air pockets to descend, thus providing oxygen for further growth. No matter whether the agar was so soft as to slide in the tubes when tilted, or whether it was comparatively hard (2 per cent), perithecia always matured a few days after the two mycelia came into contact in the presence of air. All the evidence obtained by the writer goes to show that without this contact between two mycelia of opposite sex, perithecia are not produced, and those hypothetical diffusible hormones, if any are produced by the strains of *Neurospora sitophila* and *N. tetrasperma* cultured, are not potent to induce the formation of perithecia with asci in U–tube cultures such as were described by Moreau and Moruzi.

THE NEW YORK BOTANICAL GARDEN

The genus Cinchona in Bolivia

H. H. Rusby

The most and best of our knowledge of the Bolivian cinchonas has been gained from a study of the living plants under cultivation in Bolivia and the Indies, and from that of the commercial products of these and the wild-growing trees. An important result of this study has been to demonstrate the incompleteness and insufficiency of taxonomic evidence supplied solely by the study of ordinary herbarium material. It is doubtful if any other genus of equal size has received such thorough study, as to gross and microscopical structure, chemistry, reproduction, embryology, horticulture, ecology and geography, as has *Cinchona*. It is remarkable to how great an extent the deductions from these several lines of study have been found mutually confirmatory, and the most of this evidence has been secured by a study of the trees under cultivation and by that of the commerce in the barks and their products.

In the early part of the year 1886, I devoted a number of weeks to the study of these trees in Mapiri, Bolivia, and in Yungas in 1885, and became familiar with their culture over many square miles of the Andean slopes. The very large collections then made were carefully studied as to their genetic origin as well as their individual characters, economics, and history. These specimens included ample herbarium material, four-foot quills of trunk bark—taken in each case from the same tree that yielded the herbarium material bearing the respective number—and wood-sections. Careful records were made and published in regard to the specimens, together with an account of culture, commerce and products.[1]

In the most recent publication on the Bolivian cinchonas, Standley's *The Rubiaceae of Bolivia*[2], all this information is ignored, with the result of so many errors that I can regard the publication only as a misfortune to *Cinchona* literature. On page 272 of this publication, occurs the following paragraph:

Cinchona officinalis L. Sp. Pl. 172. 1753. *C. lancifolia* Mutis, "Periódico de Santa Fe" 465. 1793. *C. nitida* R. & P. Fl. Peruv. 2:50. *pl. 191.* 1799. *C. lanceolata* R. & P. Fl. Peruv. 2:51. 1799. *C. Condaminea* Humb. & Bonpl. Pl. Aequin. 1:33. *pl. 10.* 1808. *C. macrocalyx* DC. Bibl. Univ. 41:150. 1829. *C. calisaya* Wedd. Ann. Sci. Nat. III. 10:6. 1848 (type from Bolivia). *C. amygdalifolia* Wedd., loc. cit. (described from Bolivia and Peru). *C. boliviana* Wedd., op. cit. 7. 1848 (type from

[1] Rusby, H. H. The cultivation of *Cinchona* in Bolivia. Pharm. Rec. **7**: 305–308. 1887.

[2] Standley, Paul C. The Rubiaceae of Bolivia. Field Museum Nat. Hist. Bot. Ser. **7**: 253–339. 1931.

Bolivia). *C. calisaya β calisaya vera* Wedd. Ann. Sci. Nat. III. 11:269. 1849. *C. calisaya β Josephiana* Wedd., loc. cit. *C. Condaminea δ lancifolia* Wedd., loc. cit. *C. lancifolia* var. *calisaya* Wedd. Ann. Sci. Nat. V. 12:35. 1869. *C. Forbesiana* Howard ex Wedd., op. cit. 36. 1869 (type from banks of Río Mapiri, Larecaja, at 300–1,200 m., *Forbes*). *C. calisaya* var. *microcarpa* Wedd., Ann. Sci. Nat. V. 11:361. 1869 (type from Valley of Coroico, Yungas). *C. Calisaya* var. *boliviana* Wedd., loc. cit. 1869. *C. Calisaya* var. *oblongifolia* Wedd., loc. cit. 1869 (type from Yungas). *C. Calisya* var. *pallida* Wedd., loc. cit. (type from Valley of Tipuani, Larecaja). *C. Josephiana Wedd.*, loc. cit. 1869. *C. Josephiana* subvar. *glabra* Wedd., loc. cit. 1869. *C. Josephiana* subvar. *pubescens* Wedd., loc. cit. 1869. *C. Josephiana* subvar. *discolor* Wedd., loc. cit. 1869 (type from Valley of Pelechuco). *C. Weddelliana* Kuntze, Monogr. *Cinchona* 29. 1878 (type from Bolivia). *C. Ledgereana* Moens ex Trimen, Journ. Bot. 19:323. 1881.

This is followed by the citation of thirty-two collections, all referred to *C. officinalis*, not one of which pertains to that species, which has never been found in Bolivia, either wild or under cultivation, nor in any of the extensive region that intervenes between Bolivia and the home of that species.

The number and variety of errors in these two paragraphs require classification into groups, before they can be dealt with individually. Omitting from present consideration *C. nitida*, *C. lanceolata*, *C. amygdalifolia*, *C. Boliviana*, and *C. Weddelliana*, regarding the specific identity of which there are reasonable grounds for difference of opinion, and *C. Forbesiana*, *C. Condaminea*, and *C. macrocalyx*, concerning the validity of which I have never been able to form an opinion, I submit the following confident opinions, as the result of my extensive study of the plants from different points of view, all agreeing in the conclusions which they indicate.

1. The resemblances between the narrow-leaved forms of *C. Calisaya* (which approach *C. Ledgeriana*) and *C. officinalis* are merely superficial, the two species being quite distinct in nature and habit.

2. *C. Calisaya* and *C. Ledgeriana* (which latter probably includes *C. Calisaya*, vars. *oblongifolia* and *microcarpa*) are certainly very close, and excuse the opinion that they are specifically identical. Nevertheless, under cultivation, they come true from seed and maintain their respective characteristics, and it seems preferable to treat them as two species.

3. There seem to be not even superficial characters to justify a careful student in connecting *C. Josephiana* with *C. Calisaya*, and this, in my opinion, relates to the examination of herbarium material as well as to field observations.

4. The '*C. Josephiana*, subvar. *pubescens*' cited is undoubtedly a hybrid of *C. Josephiana* and *C. ovata* (*C. pubescens* as named by Standley).

Discussing the above propositions, it is to be noted that few plants are so subject to variation between the leaves of their juvenile and mature

states as the cinchonas, a fact that will later be shown to have a bearing on the questions here discussed. There is little doubt that some of the proposed species and varieties have been based on these differences.

Of the thirty-two collections cited by Standley, ten are of my own collecting. All these were taken from cultivated trees of the plantation, and it is reasonably certain that twelve of the others are of the same origin. At the time of my stay there, no wild-grown plants of either *C. Calisaya* or *C. Ledgeriana* were obtainable, either in Mapiri or Yungas, although I offered liberal rewards to obtain them, and it seems rather inconsiderate for any botanist to venture on such radical views as those quoted above, regarding the identity of cultivated plants, without knowledge of the conditions of cultivation in the region concerned, a fact that will be more apparent when we consider other paragraphs of the paper under review.

The differences between *C. Calisaya* and *C. officinalis* are so marked, and of such great practical importance, and are so constant, that the cultivation of the latter for commercial purposes was early abandoned. A notable illustration is found in the abandoned *officinalis* plantations in Jamaica. These differences relate especially to the leaves, fruits, bark, and alkaloidal yield. The fruits of all forms of *C. Calisaya* and *C. Ledgeriana* are notable for the extreme degree of elastic curvature of the valves in dehiscence. Remaining attached at the top, and more or less at the base, the valves curve outward so that the pod, when dehiscence is complete, is often much broader than long. In *C. officinalis*, this curvature is notably slight.

The character of the leaves of *C. Calisaya* will be considered later, but it is a fact that those of *C. officinalis* are very different.

Standley says of the bark of *C. Calisaya* 'the trunk may be known by the periderm of the bark . . ., being always marked by longitudinal ridges or cracks, a characteristic remarked of no other tree of these forests, excepting one or two others of the same family.' This is his only reference to bark characteristics, attention to which has dominated the entire trade in cinchona bark previous to the establishment of testing by chemical assay. Not only was the species determined solely by the fissuring of the bark surface, but its maturity, and to a great extent its quality and value, were judged by this character. My bark specimens, now in the Museum of the Philadelphia College of Pharmacy, and my wood sections, at the New York College of Pharmacy, supply a perfect series of illustrations of this subject. It is safe to say that any purchaser of supposed *C. Calisaya* or *C. Ledgeriana* bark that possessed the exact appearance described above would lose most or all of his investment. The first and most conspicuous of the fissures appearing in the bark of these two species are circular, ap-

pearing at the nodes, where a pair of leaves had previously existed. Later, longitudinal ridges, starting as rows of warts, appear and still later crack open to form longitudinal fissures. A bark in this stage is not mature, does not contain its proper amount of quinine, and will not be accepted by a well-informed buyer, until its surface has become covered with irregular fine fissures. Because of the striking resemblance of this scaliness to that of the tarsus of a fowl, the natives have dubbed this '*pata de gallo*' bark, and this evidence of quality has been accepted and acted on generally in the bark trade. This appearance has never been seen in *C. officinalis* bark, except when it was the result of cross-pollination, which has occurred in the East Indies, though never in Bolivia, where, as stated, *C. officinalis* has not occurred. It is also true that the character of these fissures is definite and will never leave one in doubt if he is acquainted with them. Anyone visiting Sorata in the 1880's would have seen large warehouses where men were engaged in opening bark packages and examining every quill, accepting or rejecting them on the basis of the above appearance, although a certain percentage of immature bark, not having the chicken-leg appearance, would be accepted it not too thin.

The alkaloidal content of *C. officinalis* rarely exceeds 3.5 per cent, and almost three-fifths of it is quinine, while that of *C. Calisaya*, wild-grown, has reached nearly 6.5 per cent, four-fifths of it quinine. Selected bark from specially treated cultivated trees has been known to yield more than 15 per cent. The legal requirement is 5 per cent, which effectually excludes *C. officinalis* bark.

The reference of *C. Josephiana* to *C. Calisaya* is peculiarly in violation of the natural relations of the two. In 1849, Weddell published the opinion that a shrubby species of Bolivian cinchona pertained to the species *C. Calisaya*, and he named it var. *Josephiana*. This view was accepted by Markham, who based his collection of plants and seeds for introduction to cultivation in British India, on this theory. This error on Markham's part was not wholly excusable, since he had the benefit of the extensive knowledge of his associate, Charles Ledger, who had lived in the country and was thoroughly acquainted with the plants and their respective medicinal properties and commercial values. He insistently urged upon Markham the fact that the *C. Josephiana* bark was worthless and that, on botanical grounds, it was not closely related to *C. Calisaya*, and he did all in his power to induce Markham to confine his collection to the valuable species. However, the great bulk of seeds and plants carried away by Markham were of this species. It was several years after the introduction of the plants to India before the mistake was admitted, and vast plantations established in the meantime, in both British and Dutch India, were al-

most worthless, the result being the loss of hundreds of thousands of pounds sterling. In the meantime, Ledger, acting on his own responsibility, had secured a meagre supply of genuine *C. Calisaya* seeds, which he furnished to the British Government, and which were the means of saving cinchona culture from failure. One can imagine how those associated in the above events, or familiar with their history, will receive Standley's revival, in 1931, of this colossal *Calisaya-pajinal* blunder of 1849, abandoned by its author in 1869.

It is difficult to understand how so careful a botanist as Weddell could have taken the view that he did, and it is noteworthy that Ledger, who had known the plants much longer and more intimately, contested his view. Something is to be learned of this error from an examination of Weddell's types of *C. Calisaya*, which I was able to find at the home of Mr. Howard. These represent the narrow-leaved form of the species, and include only the leaves near the flowers, which are always narrower than those below. Most significant of all is the fact that in 1869 Weddell abandoned his former view, and named the plant *C. Josephiana*. He had, in the meantime, secured the benefit of the evidence afforded by cultivation, and his former view had met with universal condemnation.

Characteristic plants of *C. Calisaya* and *C. Josephiana* exhibit the following contrasts: *C. Josephiana* never grows in shaded places, but always on hot, dry, open hillsides, called *pajinals* by the people, whereas *C. Calisaya* is distinctly a forest tree. The home of *C. Josephiana* is at a much higher altitude. The altitudinal limitations of growth in this genus are decidedly narrow. When a plantation of *C. Calisaya* was allowed to extend too far up the mountainside, I have seen a very definite line of demarkation between the dead or dying trees above and the healthy ones below. It is not true, as stated by Standley, that *C. Calisaya* is sometimes shrubby. It is always a tree and will not flower until it has reached tree dimensions. *C. Josephiana*, on the other hand, never attains a height of more than ten feet, and is always of straggling habit. The bark of *C. Josephiana* is thin and never scaly, but is usually longitudinally wrinkled in drying, and never in the slightest degree resembles that of mature *C. Calisaya*. The leaves of *C. Josephiana* are usually more or less inequilateral or oblique. They never curve or wave in the wind, but are thick, rigid and coarse in texture. Those of *C. Calisaya* are conspicuously thin, of fine texture and silky appearance, and wave and curve in the wind, presenting a most beautiful appearance. Some of them being crimson on the lower surface, the effect is very characteristic. The difference in the relations of the secondary veins to the midrib are alone sufficient to distinguish the two. The flower panicles of *C. Calisaya* are large and many flowered, and droop

more or less, while those of *C. Josephiana* are stiffly erect and rigid. The flowers of the latter are larger and of different color. In the capsules, very conspicuous differences are found. Those of *C. Josephiana* are larger and relatively longer, and in dehiscence they separate at the base, but present little of the elastic curvature that is so characteristic of *C. Calisaya*. The bark of *C. Josephiana* is practically devoid of alkaloid. A cross-section of it, or even a pinch of its powder, will be instantly distinguished from that of *C. Calisaya*.

From page 273 of Standley's paper, I quote the following:

Cinchona pubescens Vahl, Skrivt. Naturh. Selsk. 1:19. 1790. *C. hirsuta* R. & P. Fl. Peruv. 2:51. *pl. 192.* 1799. *C. purpurea* R. & P., op. cit. 52. *pl. 193.* 1799. *C. ovata* R. & P., op. cit. 52. *pl. 195.* 1799. *C. cordifolia* Mutis ex Willd. Ges. Naturf. Freund Berlin Mag. 1:117. 1807. *C. asperifolia* Wedd. Ann. Sci. Nat. III. 10:7. 1848 (type from Bolivia). *C. australis* Wedd., loc. cit. 1848 (described from Bolivia and Peru). *C. purpurascens* Wedd., loc. cit. 1848 (described from Bolivia and Peru). *C. Chomeliana* Wedd., op. cit. 9. 1848 (type from Bolivia). *C. pubescens* α *Pelletieriana* Wedd. Ann. Sci. Nat. III. 11:270. 1849. *C. succirubra* Pavon ex Klotzch, Abh. Akad. Berl. 1857:60. 1858.

This is followed by a citation of collections referred to this species, together with a description of the tree. I note first, that *C. asperifolia* is here given as a synonym of *C. pubescens*, whereas on page 271, it is maintained as a species. The reference of *C. ovata* to *C. pubescens* does not appear justifiable, in view of all the evidence. That of *C. purpurascens* and *C. purpurea* appears correct. That of *C. succirubra* will probably find no support anywhere. The author correctly describes the trunk of *C. ovata* as about 30 cm. in diameter, whereas *C. succirubra* is a very large tree, becoming nearly two yards in diameter. Because of its great size, it is now used in the Orient as a stock for grafting with *C. Ledgeriana*. The resulting tree acquires the dimensions of the host, while retaining the alkaloidal yield of the scion. It chanced that a small plantation of *C. succirubra* grew in Yungas, where I remained for some time, being the only one in Bolivia. I was thus able to compare it with *C. ovata*, the predominant species of northern Bolivia. The two have nothing in common, with the exception of their hairy leaves, and the trichomes of the two could not be mistaken for one another. Standley quotes early writers in saying that *C. ovata* yields a valuable bark, but this statement was erroneous from the beginning. This bark is the 'Cocola' of the collectors, and was valued only for fraudulent sale to ignorant buyers. It is very thin and not at all fissured, and contains scarcely any alkaloid, perhaps none when not of mixed parentage. The bark of *C. succirubra*, on the contrary, contains up to 6 per cent of alka-

loid, about two-fifths of it quinine. The bark of *C. succirubra* is heavily ridged, but never longitudinally fissured. These different types of bark are perfectly illustrated in the National Standard Dispensatory. In all my acquaintance with *C. ovata*, I have never seen a truly cordate leaf upon it, a character which Standley attributes to it. The base of this leaf is very abruptly contracted into a broad petiole, which is always more or less margined by the produced base.

In his citation of collections, Standley has reported those of the same origin, some under '*C. officinalis*' (*C. Calisaya*) and others under '*C. pubescens*' (*C. ovata*). These are all hybrids of *C. ovata* with other species, mostly with *C. Calisaya*.

This subject of hybridity has not been touched upon in the paper under discussion, yet it represents the most important condition that has affected cinchona culture in Bolivia. This condition has not been active in the East Indies, doubtless because those plantations are not surrounded and intruded upon by wild cinchonas of other species. In the production of seeds, Bolivian planters have been obliged to resort to unusual methods to prevent the access of foreign pollen, the seed trees being planted in remote situations, and protected in various ways, yet I have never seen these efforts to avoid cross pollination completely successful. The plantations are mostly stocked by contract, the contractor not being released and fully paid until the trees have reached an age when their specific identity can be verified. The seed-beds are culled as fast as the young hybrids can be identified, but the evidences of hybridity increase with age. After transfer to the plantation, the trees are allowed to grow to a height of about six feet, when arbitrators are appointed to determine the number of acceptable trees, and the contractor is paid for these only. The arbitrators walk between the rows, plucking a leaf from each tree. In the evening, these leaves are examined in joint session, and those are counted out which are not acceptable. Identification is based almost wholly on the presence of pubescence upon the leaves. The leaf of neither *C. Calisaya* nor *C. Ledgeriana* is ever hairy, except through cross pollination. Furthermore, the degree of pubescence has been found to agree closely with the character of the bark surface and its thickness, and with the alkaloidal yield. For this reason, the arbitrators do not reject leaves showing slight pubescence, and the bark buyers accord similar consideration to bark of reasonable thickness, even though not fully scaly. It is thus not only hybridity, but the degree of it that determines the decision.

The methods of pure science are not always as correct or conclusive as they are 'pure'. When pure science reaches conclusions that are directly opposed to the findings of legitimate commerce, it is up to the scientist to

ascertain the cause of the difference, and not to persist in declaring that two things which are quite different are the same!

The determination of hybridity between *C. Calisaya* and *C. Josephiana* is not so easy, because both are glabrous, but I feel very confident that some of the narrow-leaved species that have been described from Bolivia are based on such hybrids, and I have determined some of my own collections as products of this cross-pollination.

At the present time, the Bolivian plantations are abandoned, a result of cheap oriental competition. In the meantime, the wild trees have continued to propagate, and in 1921, I found the forests again filled with cinchona trees.

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Propagation of Equisetum from sterile aerial shoots[1]

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The process of differentiation of the cells of a multicellular organism into somatic and reproductive systems has been an important problem for investigation and speculation for many years. Formerly, before the more exact knowledge of heredity was attained, the extreme speculations of Weismann largely dominated biological thought, especially on the zoological side. Even at the present time many treatises on general biology and genetics still present these purely speculative hypotheses, even though it is evident that they were developed before biologists had a proper knowledge of the reproductive process, or of karyokinesis and the reduction division.

The following experiments were undertaken for the double purpose of discovering how readily species of *Equisetum* could be propagated from aerial, sterile shoots and of obtaining evidence which would throw light on the problem of differentiation in relation to the reproduction of the individual.

The higher species of *Equisetum* are especially favorable plants for such a study of differentiation since they have highly dimorphic aerial, fertile and sterile shoots coming from the rhizome. In the lower species there is practically no difference between the sterile and fertile shoots, except that the latter have cones and the former have none, although they may develop cones later on lateral branches. The differentiation of the terminal buds of the aerial shoots takes place only near the end of their ontogenetic development. In the highest species, like *E. arvense* L., there is a tetramorphic development of the stem, besides the highly specialized tubercles on the rhizome. There is not only an extreme vegetative dimorphism between the sterile and fertile shoots, but the two kinds of shoots are differentiated as such at the very beginning of their development as lateral buds from the rhizome.

In the winter of 1929–30, Mr. Glenn W. Blaydes, of the Botany Department, called my attention to some aerial shoots of *E. praealtum* Raf. which had developed roots from the submerged nodes after being placed for some time in a jar of water. Accordingly this species of scouring-rush was used for the first experiment. Large shoots, both sterile and fertile, gathered in April, were cut off at the third or fourth internode above the ground and placed in jars of water with a little earth in the bottom. The

[1] Papers from the Department of Botany, The Ohio State University, No. 280.

submerged internodes promptly developed both roots and branches abundantly. In May they were planted in large flower pots and the pots were placed with their bottoms in water and left thus for the summer. By the latter part of September the cuttings had developed numerous rhizomes with many good-sized aerial shoots. Some of the rhizomes were over 3 ft. long and several of the new aerial shoots from them were $1\frac{1}{2}$ ft. high. The rhizomes grew around the inner walls of the pots about 2–3 inches from the surface.

It is thus an easy matter to grow plants of *E. praealtum* from the green sterile shoots. The aerial green branches which come from the nodes of the green shoots, as well as those which develop from the rhizome, show a very strong negative geotropism in this species. They are strongly differentiated from the rhizome in their physical reaction as well as morphologically. The aerial environment with exposure to light determines green determinate shoot development with vertical growth, while the dark underground environment determines black, indeterminate shoots, or rhizomes with horizontal growth, as well as green determinate shoots.

In the experiments with the cuttings, vertical green shoots were developed so long as the plants were in the water exposed to light, but when the cuttings were planted in earth the same internodes developed horizontal rhizomes. The differentiation of the original shoot into a characteristic, green, negatively geotropic system was not at all at the expense of the potentialities which produce black diageotropic systems. The differentiation is not at the expense of any hereditary potentialities possessed by the protoplast. Dedifferentiation is complete in either direction under a proper environmental change.

Having attained success in the vegetative propagation of *E. praealtum*, the same general methods were tried with the much more extremely specialized *E. arvense* L. This species has very extremely differentiated fertile and sterile shoots, and these shoots are differentiated from the very beginning of their development from the rhizome. Cuttings of aerial, green, sterile shoots were made October 4, 1930. These were comparatively small shoots and were in good condition for the time of the year, having not yet been frosted. A dozen shoots were placed in gallon crocks, filled about two-thirds with soil and sand. The ends of the shoots were stuck about half an inch into the soil and the crock was then filled nearly to the top with water. The water was changed from time to time in order to prevent the growth of fungi and bacteria on decaying branches. Eight of the cuttings produced new sprouts. After seven weeks, when they were well along the way in producing roots, the water was poured off, more soil added to cover the roots, and after this the soil was kept constantly water-soaked.

On December 1st, they were put into continuous light and continued to grow well, although very slowly, until March 12, when they were examined for rhizome development. All had produced rhizomes and tubercles and aerial green shoots from the rhizomes. The tubercles were packed with large starch grains and covered with long brown epidermal hairs. The branched aerial shoots were up to 8 inches high and some of the rhizomes were over 2 feet long, growing around the inner walls of the crocks. The rhizome produces no whorl branches but only sporadic main branches of two kinds from the nodes, aerial green shoots which grow against the direction of gravity and black rhizome branches which grow more or less horizontally under the ground.

The readiness with which new plants could be propagated from the main stems of the sterile aerial shoots of *E. arvense* suggested that new plants might also be produced from the small, highly specialized, 3- and 4-angled whorl branches. Accordingly, on May 25, 1931, such branchlets, each about 4–6 inches long, were planted about 2 inches deep in sandy soil, in large flower pots which were then placed in jars of water filled up to the level of the soil in the pots. The plant cuttings were kept in continuous light for three weeks, a 100 watt electric light bulb being used at night. Some of the branchlets began to develop lateral buds in ten days. There were 32 planted branchlets originally, and of these 23 sprouted side branchlets and roots and 17 of them survived and finally developed rhizomes. After three weeks the pots were transferred to a water tank with their bases about 3 inches in the water and received no more light at night.

The plants made a good growth during the summer, and by August 29 some had rhizomes up to 20 inches long with numerous roots and young aerial green shoots and were still growing vigorously. Some plants had also begun to produce tubercles. The original 3- and 4-angled branchlets remained unchanged in general character, except that they changed to a brown color where covered with the soil. Most of the original branchlets had in the meantime died off above ground, although the portion in the soil from which the rhizomes were developed was still alive.

These whorl branchlets of *Equisetum* represent the extreme vegetative differentiation of the sterile shoot, and do not produce semisterile cones, such as rarely occur on the main axis of the shoot. These tiny branchlets differentiated into determinate, annual, sterile shoots have thus not lost one particle of their original hereditary potentiality in the process of differentiation.

The branching system of *Equisetum* apparently evolved in the following manner: (1) stem not branching and completely indeterminate in growth; (2) sporadic lateral branching along with rhizome development,

the aerial branches developing as slowly determinate shoots at first and later evolving into promptly determinate shoots; (3) whorl branches evolved which were expressed only on the aerial shoots; (4) inhibition of the whorls on all the aerial shoots in some phylogenetic lines and inhibition of whorls only on the reproductive shoot in the highest series to which *E. arvense* belongs. Along with inhibition of branches in the *E. arvense* line came the extreme dimorphism, with loss of chlorophyll and a very short aerial life for the reproductive shoot. Somewhere along the evolutionary sequence, tubercle development was added. Thus a very complex and highly specialized hereditary reaction system is present in the cells and every protoplast in the plant has all the hereditary potentialities.

Now the problem arises as to how the process of differentiation of the various branch systems is brought about. It must be through the development of physiological states and gradients in relation with the environment. As stated in the beginning, many biologists apparently still have an abiding faith in the Weismannian speculations, although it is true that these hypotheses never made much headway among botanists. For it was well known that in the early embryonic development of the higher plants two very diverse structural and reaction systems, the root and the shoot, are developed. The reproductive continuity is normally through the shoot while the usual root never gives rise to reproductive cells, either in its phylogeny or in its ontogeny. It is purely a somatic system in its usual reactions. Yet very commonly the root can be made to produce a shoot which finally develops reproductive cells. This extreme differentiation of the body into root and shoot, therefore, was not brought about by a segregation of 'germplasm' and 'somatoplasm' nor by a change of 'germplasm' into 'somatoplasm.' The root cells have exactly the same kind of fundamental hereditary mechanism as the shoot cells and their descendants, the reproductive cells of one sort or another. There has been no change of 'germplasm' into 'somatoplasm' in the differentiation of the root into its peculiar structures, and physical and physiological reactions. The root has a 'germ track' as well as the shoot, although it was never in evidence during the geological ages. It is thus plain that, in such changes as root to shoot, or sterile, aerial shoot to rhizome, we have evidence that a plant or an animal soma may be 'born again' if only the right environment and conditions are supplied.

The Nussbaum-Weismann theory of heredity dates back to about the year 1880, when Nussbaum emphasized the genetic continuity of the germ cells from generation to generation, stating that during development the fertilized egg divides to produce on the one hand the cell material of the individual body and on the other the cells by which the characters of the

species are maintained. 'The fertilized egg, accordingly, divides into cells that constitute the individual and cells for the maintenance of the species.' This notion of the cells dividing into two types is the fundamental fallacy of the assumption. They sooner or later differentiate into distinct reaction units, but the reproductive cells are often differentiated as extremely or even more so than the ordinary body cells, and in both the higher plants and animals usually are not able to continue growth without a special stimulus or condition which is then supplied through conjugation or other means. The same confusion of analysis was formerly quite commonly expressed in relation to the reduction division, which was supposed to be a process by which the cell got rid of something that another mechanism might be supplied through fertilization.

In 1883 Weismann published the first of his speculative essays on heredity, and for many years Weismannism dominated various schools of speculative biological thought, although the whole structure was largely based on negative evidence and on the prevalent ignorance of the time. The terms, 'germplasm' and 'somatoplasm' can lead only to wrong conceptions of the ontogenetic process. Every protoplast that continues to function is a potential 'germ cell'. The common aphorism that 'an egg can produce a new hen or a new egg but a hen cannot produce a new hen or a new egg' is a fundamental fallacy based on an imperfect knowledge of living organisms in general and the nature of the differentiation process in particular.

Every one recognizes the fact that some cells may become so extremely differentiated that they do not return to the embryonic activity under ordinary or even the most extreme conditions, but the problem is one concerning the nature and degree of differentiation and the stimulation to dedifferentiation rather than the division or segregation of 'somatoplasm' from 'germplasm' by any process of change of the protoplast. Thus the study of plants like *E. arvense* may aid decidedly in eliminating such fantastic conceptions as 'germplasm', 'somatoplasm', and 'germ track' from the biologist's vocabulary.

COLUMBUS, OHIO

INDEX TO AMERICAN BOTANICAL LITERATURE
1927–1931

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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